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COASTAL ENVIRONMENTAL GRADIENTS – KEY TO REPRODUCTION HABITAT MAPPING OF FRESHWATER FISH IN THE BALTIC SEA

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II Kallasvuo, M., Salonen, M., Lappalainen, A. 2010: Does the zooplankton availability limit the larval habitats of pike in the Baltic Sea? Estuarine, Coastal and Shelf Science 86: 148–156.

III Härmä, M., Lappalainen, A., Urho, L. 2008: Reproduction areas of roach (*Rutilus rutilus*) in the northern Baltic Sea: potential effects of climate change. Canadian Journal of Fisheries and Aquatic Sciences 65: 2678–2688.

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ABSTRACT

Habitat requirements of fish are most strict during the early life stages, and the quality and quantity of reproduction habitats lays the basis for fish production. A considerable number of fish species in the northern Baltic Sea reproduce in the shallow coastal areas, which are also the most heavily exploited parts of the brackish marine area. However, the coastal fish reproduction habitats in the northern Baltic Sea are poorly known.

The studies presented in this thesis focused on the influence of environmental conditions on the distribution of coastal reproduction habitats of freshwater fish. They were conducted in vegetated littoral zone along an exposure and salinity gradient extending from the innermost bays to the outer archipelago on the south-western and southern coasts of Finland, in the northern Baltic Sea. Special emphasis was placed on reed-covered *Phragmites australis* shores, which form a dominant vegetation type in several coastal archipelago areas. The main aims of this research were to (1) develop and test new survey and mapping methods, (2) investigate the environmental requirements that govern the reproduction of freshwater fish in the coastal area and (3) survey, map and model the distribution of the reproduction habitats of pike (*Esox lucius*) and roach (*Rutilus rutilus*).

The white plate and scoop method with a standardized sampling time and effort was demonstrated to be a functional method for sampling the early life stages of fish in dense vegetation and shallow water. Reed-covered shores were shown to form especially important reproduction habitats for several freshwater fish species, such as pike, roach, other cyprinids and burbot, in the northern Baltic Sea. The reproduction habitats of pike were limited to sheltered reed- and moss-covered shores of the inner and middle archipelago, where suitable zooplankton prey were available and the influence of the open sea was low. The reproduction habitats of roach were even more limited and roach reproduction was successful only in the very sheltered reed-covered shores of the innermost bay areas, where salinity remained low (< 4‰) during the spawning season due to freshwater inflow. After identifying the critical factors restricting the reproduction of pike and roach, the spatial distribution of their reproduction habitats was successfully mapped and modelled along the environmental gradients using only a few environmental predictor variables.

Reproduction habitat maps are a valuable tool promoting the sustainable use and management of exploited coastal areas and helping to maintain the sustainability of fish populations. However, the large environmental gradients and the extensiveness of the archipelago zone in the northern Baltic Sea demand an especially high spatial resolution of the coastal predictor variables. Therefore, the current lack of accurate large-scale, high-resolution spatial data gathered at exactly the right time is a considerable limitation for predictive modelling of shallow coastal waters.

TIIVISTELMÄ

Lisääntymisen onnistuminen vaikuttaa olennaisesti kalapopulaation kokoon ja määrää syntyvän vuosiluokan vahvuuden. Kalojen ympäristövaatimukset ovat suurimmat varhaisissa elinvaiheissa ja siksi lisääntymisalueiden laadulla ja laajuudella on olennainen merkitys kalakannan tuotolle. Useiden pohjoisella Itämerellä esiintyvien kalalajien kutualueet sijaitsevat matalilla alueilla jopa alle parin metrin syvyydessä ja useimmiten myös pienpoikaset hyödyntävät samoja matalia alueita. Kalojen lisääntymisalueista rannikolla ja saaristossa ei kuitenkaan ole systemaattisesti kerättyä kattavaa tietoa. Tämä johtuu pitkälti menetelmiin liittyvistä puutteista ja kartoitettavien rannikkoalueiden laajuudesta.

Väitöstutkimus käsittelee ympäristötekijöiden vaikutusta makeanveden kalojen lisääntymisalueiden sijaintiin ja laajuuteen Suomen lounais- ja etelärannikon matalilla kasvillisuusrannoilla. Tällä rannikkoalueella saaristovyöhykkeiden ja -alueiden välillä on suuria eroja mm. avoimuudessa ja veden suolapitoisuudessa. Erityishuomiota kiinnitettiin ruovikkorantoihin, jotka muodostavat keväisin vallitsevan kasvillisuustyypin alueen matalilla rannoilla. Tutkimuksen kolme päätavoitetta olivat: (1) kehittää ja testata uusia kenttäkartoitusmenetelmiä sekä lisääntymisalueiden mallinnusmenetelmiä, joiden avulla rajatuilla alueilla tehtyjen kenttäkartoitusten tuloksia yleistetään laajemmille alueille, (2) tutkia rannikolla lisääntyvien makeanveden kalojen lisääntymisvaiheen ympäristövaatimuksia ja (3) kartoittaa hauen ja särjen lisääntymisalueita ja tuottaa mallien avulla koko tutkimusalueen kattavat lisääntymisaluekartat.

Tärkeimpänä poikasnäytteenottomenetelmänä käytettiin valkolevyä ja kauhaa vakioidulla kartoitusponnistuksella. Menetelmä osoittautui toimivaksi ja sen avulla voidaan kartoittaa pienten kalanpoikasten esiintymistä matalassa vedessä ja tiheässä kasvillisuudessa. Tulosten perusteella ruovikkorannat ovat erittäin tärkeitä kutu- tai poikasalueita useille rannikon kalalajeille, kuten mateelle, hauelle, särjelle ja monille muille särkikaloille. Hauen lisääntymisalueista valtaosa sijaitsi sisä- ja välisaariston suojaisilla ruovikkorannoilla, joissa sopivaa eläinplanktonravintoa oli tarjolla ja avomeren vaikutus oli pieni. Erityisen paljon hauen mätiä ja pienpoikasia esiintyi ruovikkorannoilla, joissa kasvoi myös vesisammalta. Särjen lisääntymisalueet olivat rajoittuneet sisemmäksi saaristoon ja särjen lisääntyminen onnistui käytännössä ainoastaan sisälahtien ruovikkorannoilla, jotka olivat selkeästi jokien ja purojen tuoman makeanveden vaikutuspiirissä ja missä veden suolapitoisuus alkionkehityksen aikana oli alle 4 ‰. Hauen ja särjen lisääntymisalueiden sijainti laajalla rannikkoalueella onnistuttiin mallintamaan vain muutamaa ennustemuuttujaa käyttämällä hyödyntäen kattavaa kalanpoikasten kenttäkartoitusaineistoa, paikkatietomenetelmiä ja ympäristömuuttujakarttoja.

Tärkeiden lisääntymisalueiden sijaintia kuvaavat kartat ovat osoittautumassa tärkeäksi työkaluksi niin rannikkoalueiden käytön suunnittelussa ja suojelussa kuin kalakantojen kestävässä hoidossa. Pohjoisen Itämeren rannikkoalueiden rikkonaisuus ja ympäristömuuttujien suuret vaihteluvälit eri saaristovyöhykkeissä aiheuttavat sen, että lisääntymisalueiden mallinnuksessa käytettävien ympäristömuuttuja-aineistojen alueellisen erottelukyvyn tulisi olla korkea. Tällä hetkellä riittävän tarkkojen ja oikeaan aikaan kerättyjen ympäristömuuttuja-aineistojen puute kuitenkin rajoittaa lajien eri kehitysvaiheiden esiintymisen mallintamista matalalla rannikkoalueella.

INTRODUCTION

FISH REPRODUCTION

The success of the reproductive phase, i.e. the distribution and abundance of the early life stages of fish, determines the adult population size (Houde 1989, Wahle and Steneck 1991). The habitat requirements of fish are known to be most strict during the early life stages, and the quality and quantity of reproduction habitats lays the basis for fish production (Urho 2002a). A good reproduction habitat maintains appropriate abiotic environmental conditions, and also contains suitable prey organisms and a sufficiently low density of competitors and predators for the eggs and larvae to survive and successfully recruit to juvenile and adult populations (Leggett and Deblois, 1994, Urho 1996). However, coastal areas consist of several types of habitat and the habitats suitable for reproduction vary between species and are always limited compared to the entire distribution of a fish species (Urho 2002a).

The reproductive phase in fishes includes embryonic, larval and juvenile periods (Chambers and Trippel 1997, Kovac and Copp 1999, Urho 2002b). The larval period begins at hatching, already before the onset of exogenous feeding (Hubbs 1943), and lasts until the metamorphosis has come to an end, the juvenile becomes scaled and resembles the adults of its species (Rass 1946). In the research presented in this thesis, I have concentrated on the environmental requirements and habitats of the egg and larval stages, especially of the newly-hatched larvae, and refer to them as the "early life stages of fish". Furthermore, during the reproductive phase, the habitat of fishes can be divided into spawning, larval and nursery habitats (Urho 2002a). The spawning habitat is the specific area where the eggs are laid and, for the non-pelagic spawners, embryological development takes place. After hatching, the surrounding environment of the larvae is called the larval habitat. Determination of this environment depends not only on the location of the spawning grounds, but also on the distribution tactics of the larvae (Urho 2002b). At least two different dispersal mechanisms exist: immediate dispersion after hatching, and delayed gradual dispersion after a passive early larval phase (Hunter 1980, Urho 2002b), which is a typical dispersal mechanism for the species, such as pike (*Esox lucius*) and roach (*Rutilus rutilus*), studied here. Therefore, their spawning and larval habitats can be the same or exist very close to each other, and are here referred to as the "reproduction habitat". The habitat where young-of-the-year juveniles occur is further called the nursery habitat, and unlike in some other studies, it is not included in the reproduction habitat in this thesis.

MAPPING OF FISH REPRODUCTION HABITATS IN MARINE ENVIRONMENTS

In several sea areas around the world, both national and international efforts are aiming at identifying essential fish habitats (EFH), i.e. areas or volumes of water and bottom substrates that provide the most favourable habitats for fish populations to spawn, feed and mature throughout their life cycle (Cross et al. 1997), and more specifically, the even more restricted reproduction habitats that have high importance for fish production. However, due to differences between fish species regarding reproductive behaviour, life-history traits and habitat requirements for spawning and larval periods (Kryzhanovsky 1948, 1949, Balon 1975, 1981), several study approaches also exist. The majority of marine fish species have evolved life cycles involving pelagic egg or larval stages that have the capacity to be transported long distances, and currents therefore also have a pronounced effect on the drift and distribution of the pelagic fish eggs and larvae before metamorphosis and settlement (Harden-Jones 1968, Grosberg and Levitan 1992, Peck et al. 2009). Mapping and modelling approaches to marine fish reproduction habitats have therefore typically utilized data sets from pelagic ichthyoplankton monitoring surveys. Observations on the occurrence of the early life stages have been linked to hydrological models and abiotic or physical predictor variables, such as sea surface temperature, salinity and depth with a spatial resolution commonly > 1 km. In addition to the modeling techniques where the changes in the averaged characteristics of a fish population are simulated, also individual-based models (IBM) coupled with 3D dispersion models have been utilized to study the dispersion of eggs and larvae of marine fish (e.g. Allain et al. 2007, Peck et al. 2009). Fish reproduction habitat studies have been conducted in various marine environments, such as the Atlantic (Eastwood et al. 2001), Indian (Reiss et al. 2008) and Pacific Oceans (Neira et al. 2009), in inland sea areas such as the Mediterranean Sea (Schismenou et al. 2008), and in estuaries such as Chesapeake Bay (North and Houde 2004). These studies have often been conducted on a very large scale, although it would often be more meaningful to concentrate efforts on surveying and mapping areas where essential fish habitats are most restricted (Parrish et al. 1997). Therefore, due to the pelagic nature of the early life stages of many marine fish species, mapping and modelling efforts have often focused on surveying the less mobile, already settled young-of-the-year and juvenile stages (e.g. Le Pape et al. 2003).

However, not all fish species have pelagic early life stages, but they may be substrate spawners or have larval stages that require shelter, for instance in the form of vegetation (Kryzhanovsky 1948, 1949, Balon 1975, 1981). Typically, most freshwater fish species are demersal substrate spawners. These types of life histories pose challenges to survey methodology, since adhesive or hidden early life stages are laborious to sample. Therefore, habitat mapping and modelling studies on the non-pelagic early life and older larval stages of fishes, such as those conducted by Bergström et al. (2007) and Snickars et al. (2010), have been rare. The survey target, however, depends on the objects of the study. If a survey aims at mapping the actual reproduction habitats of fish, the focus should be either on the sampling of eggs or of newly-hatched larvae. Using newly-hatched fish larvae as survey objects has some benefits compared to fish eggs, since the newly-hatched fish larvae (1) are often relatively easier to sample than adhesive or hidden fish eggs (Backiel and Welcomme 1980), (2) often still occur close to the actual spawning and hatching grounds (Backiel and Welcomme 1980), and (3) their survival is of great importance to the fish year-class strength (Cushing 1990).

PREDICTIVE SPATIAL DISTRIBUTION MODELLING

Traditional surveys on the occurrence of the early life stages of fish aim at producing maps that show the abundance of the early life stages at the sampled sites and, for example, temporal variation in abundance between survey occasions. Predictive spatial distribution modelling, however, aims at expanding the survey result to a continuous map layer also showing the probability of occurrence of the early life stages in areas outside the actual sampling sites. Therefore, the environmental conditions suitable for a study species are first characterized, i.e. statistical models of species-environment relationships are constructed, and the distribution of these environments in space is then identified by combining the models with maps of the environmental variables in a geographic information system. The modelling outcome is a continuous probability map that is static and probabilistic in nature (Guisan and Zimmermann 2000).

With the development of new statistical

techniques and geographic information system tools, the use of predictive spatial distribution models has rapidly increased in ecological mapping in the last couple of decades (Lek and Guegan 1999, Guisan and Zimmermann 2000, Guisan and Thuiller 2005). A variety of statistical techniques have been used to relate the geographical distribution of species or habitats to their present environment, and the common ones include techniques such as ordinary multiple regression and its generalized form (GLM), logistic regression, neural networks, ordination and classification methods, Bayesian models, generalized additive models (GAM), environmental envelopes and combinations of these models (Guisan and Zimmermann 2000, Guisan and Thuiller 2005). The selection of an appropriate modelling approach is always limited by the data set, and the resulting modelled probability maps are often similar, despite using different models (Guisan and Zimmermann 2000). The selection of the model should depend on statistical considerations, i.e. the accuracy and type of data, ecological knowledge and conceptual consideration, i.e. optimizing accuracy versus optimizing generality (Guisan and Zimmermann 2000, Valavanis et al. 2008). Accuracy can often be increased by adding predictor variables in the model, but on the other hand, it may decrease the generality of the model. In optimizing generality, it is important to select appropriate predictor variables and to design an appropriate procedure for model selection. Ecological knowledge combined with statistical consideration should be used when choosing the predictor variables (Guisan and Zimmermann 2000), keeping in mind their availability, spatial resolution and direct/indirect influence on the explanatory variable. Spatial resolution may range from low (> 1000 m) to moderate (200–500 m) and high (0.5–35 m) and adequate resolution depends on the objectives of the study and on the scale of the analysis. To test the accuracy of the models, methods such as threshold-independent measures (e.g. receiver operating characteristics plots), resampling techniques (e.g. bootstrap, cross-validation) and external validation have been introduced (Guisan and Zimmermann 2000). Model validation is of fundamental importance (Olden et al. 2002) and can be conducted in a variety of ways, but the objectives of the study should define the evaluation measures used (Fielding and Bell 1997). Testing of the model in space and time will enable definition of the range of applications and the geographical transferability for which the model predictions are suitable.

Originally, predictive spatial distribution modelling was mainly used in terrestrial ecology, typically when simulating the spatial distribution of terrestrial plant (Hill 1991, Huntley et al. 1995, Franklin 1998) and animal species (Augustin et al. 1996, Mace et al. 1999, Mladenoff et al. 1999). Furthermore, it has been used as a tool to assess the impact of accelerated land use and other environmental changes on the distribution and biogeography of organisms (Kienast et al. 1996, Kienast et al. 1998, Leathwick 1998), and for establishing conservation priorities (Margules and Austin 1994, Tapia et al. 1995, Ko et al. 2009). Nowadays, in addition to these uses, a wide array of predictive spatial distribution modelling approaches have been developed as tools in climate change research (Meynecke 2004, Garzon et al. 2008) and habitat or species management (Braunisch and Suchant 2007, Tomas and Olea 2009), and both theoretical as well as practical applications have been generated (Guisan and Zimmermann 2000, Guisan and Thuiller 2005).

The extensive spatiotemporal variability that characterizes dynamic and open marine ecosystems presents difficulties for the development of predictive spatial species-habitat distribution models (Valavanis et al. 2008). In the aquatic environment, it is often more challenging to obtain good, high-resolution data on spatial predictor variables in a geographic information system compared to the terrestrial environment, and the development of marine predictive mapping and modelling approaches has therefore been considerably slower. However, an increasing number of predictive models have recently been applied in aquatic studies to predict, for example, the spatial distribution of freshwater and marine macrophytes (Lehmann 1998, Schmieder and Lehmann 2004), the presence and abundance of intertidal communities (Zacharias et al. 1999), and fish distribution and abundance both in freshwaters (Olden and Jackson 2002, Behrouz et al. 2006 and references therein, Kimura et al. 2006) and in marine waters (Francis et al. 2005, Bellido et al. 2008, Hazin and Erzini 2008). Overall, these models have performed successfully with reasonable to excellent accuracy and predictive power, despite their variable scales. A common feature of these frequently logistic modelling approaches has been that abiotic environmental conditions, such as bathymetry, wave exposure, bottom sediment type, current velocity, water temperature and salinity, have been used as predictor variables due to their better availability compared to biotic spatial predictors. Biotic factors, such as competition for food and space or predation pressure, certainly affect the reproduction success, but are difficult or even impossible to obtain as continuous maps.

ENVIRONMENTAL CONDITIONS AND FRESHWATER FISH REPRODUCTION IN THE NORTHERN BALTIC SEA

The coastal areas of the brackish northern Baltic Sea differ considerably from most other sea areas around the globe. The coastal areas of the northern Baltic Sea consist of extensive and shallow archipelagos, where the coastline is indented and long, the sea is covered with ice in the winter months, and tides and strong sea currents are essentially absent (Segerstråle 1957, Voipio 1981). At regional scale, the coastal zone can further be divided into inner, middle and outer archipelago zone. The environmental conditions vary between different parts of the archipelago gradient, and towards the outer parts the water to land ratio increases, the average size of islands decreases, exposition increases and the environmental conditions become harsher compared to the sheltered inner archipelago zone (Granö et al. 1999, Tolvanen et al. 2004). Also due to substantial freshwater inflow from rivers and the complex and wide archipelago zone, large environmental gradients in salinity, temperature and turbidity exist in the area from the inner bays to the outer archipelago. These oceanographical and hydrological conditions have an influence on the ecology and fish populations of the sea area. One special characteristic of the northern Baltic Sea is that both marine and freshwater fish occur there. Freshwater fish species form a substantial part of the fish communities in the brackish coastal areas (Ådjers et al. 2006), and more than 20 freshwater fish species are also capable of reproducing there (Urho and Lehtonen 2008). Furthermore, the majority of these freshwater fish species spawn in spring or early summer and use estuaries and shallow (< 10 m) archipelago areas for reproduction (Urho et al. 1990).

The fish reproduction habitats in the northern Baltic Sea are, however, not well known. There has been a clear lack of systematically collected data on the reproduction habitats of fish, especially of freshwater fish, in the coastal area of the northern Baltic Sea. One main reason for this is the scarcity of suitable survey methods. Some rather extensive traditional surveys on the early life stages of marine fish, such as Baltic herring (*Clupea harengus membras*), have been conducted (e.g. Raid 1985, Parmanne and Sjöblom 1988), but recently, during the 21st century, new national and international projects have finally begun to study and systematically map underwater habitats and also fish reproduction and nursery habitats (e.g. BALANCE, VELMU, PREHAB). The basic reproductive biology of many coastal fish with a freshwater origin has also been widely investigated in freshwaters (Backiel and Welcomme 1980), but the results from lakes are not directly applicable to the coastal brackish environment due to considerable differences in the environmental conditions, e.g. in temperature, salinity and water level variations.

AIMS OF THE THESIS

The research reported in this thesis forms a part of the Finnish Inventory Programme for the Underwater Marine Environment (VELMU), and was one of the first attempts to systematically produce predictive spatial distribution maps of fish reproduction habitats in the coastal areas of the northern Baltic Sea. The main focus was to examine the influence of environmental conditions on the distribution of the early life stages of fishes along vegetated littoral shores. Special emphasis was laid on reed-covered *Phragmites australis* shores, which form a dominant vegetation type in the archipelago areas on the south-western and southern coasts of Finland (Roosaluste 2007). The main study species were common freshwater fish species, such as pike and roach, which are known to prefer sheltered and vegetated littoral areas for reproduction (Holčik and Hruška 1965, Lange and Dmitriyeva 1973, Casselman and Lewis 1996, Bry 1996, Mann 1996, Urho et al. 1990). The early life stages of these species do not have pelagic dispersal mechanisms, but the newly-hatched larvae instead remain close to the shallow spawning sites (Holčik and Hruška 1965, Lange and Dmitriyeva 1973, Casselman and Lewis 1996, Bry 1996, Mann 1996, Urho et al. 1990) and spend at least the beginning of their first summer within the same vegetated habitat (Raat 1988). Therefore, the distribution of the reproduction habitats (i.e. spawning and larval habitats) of these species can be investigated by defining the critical factors limiting the distribution of the early-life stages, i.e. eggs or newly-hatched larvae.

The three main aims of this research were to:

1. Develop and test new survey methods, including both field sampling methods and tools combining statistical modelling approaches with a geographic information system (GIS) to extrapolate the obtained field observations to larger areas by utilizing environmental data collected by remote sensing methods (**I, III, IV**).

2. Investigate the environmental requirements that govern the distribution of the reproduction habitats of freshwater fish in coastal areas, the main focus being on the early life stages of pike **(I, II, IV, V**) roach (**III**, **IV**, **V**) and few other spring-spawning cyprinids (**V**). The hypothesis was that both abiotic (e.g. salinity, exposure, temperature, turbidity) and biotic factors (e.g. vegetation, prey availability) have a decisive role in determining the extent and location of reproduction habitats of freshwater fish on the south-western and southern coasts of Finland, and differences between fish species are noticeable. Environmental conditions such as vegetation and abiotic factors differ both temporally and spatially in various archipelago zones, and it was therefore hypothesized that only part of the archipelago area is suitable as a reproduction habitat for a particular species.

3. Map and spatially model the distribution of the key reproduction habitats of pike and roach in the coastal area of the northern Baltic Sea (**III, IV**), and to produce a new type of easy-to-access and cost-effective species-specific spatial information on the distribution of the essential fish habitats for coastal planning and management purposes. It is not possible to survey the extensive coastal areas solely by field surveys, and efforts are therefore needed to generalize the field observations as verified predictive spatial species-habitat distribution maps. The substrate spawning fish species were hypothesized to be well suited to predictive spatial distribution modelling.

MATERIAL AND METHODS

DESCRIPTION OF THE STUDY AREA

The study area was located on the south-western and southern coasts of Finland (59.7–60.7ºN, 21.2–26.2ºE), in the northern Baltic Sea (Fig. 1). The complex and extensive archipelago was a special characteristic of this area, and the inner bays were sheltered by several small islands. Various environmental factors such as turbidity, salinity, temperature and littoral vegetation differed both spatially and temporally in the various archipelago zones. Moreover, strong environmental gradients existed from the inner bays to the outer archipelago, e.g. Secchi depth increased from less than 1 m to almost 10 m (Fig. 2) and salinity from almost 0‰ to more than 6‰ (Fig. 3). Nowadays, reed belts are a dominant vegetation type in sheltered, soft-bottomed littoral shores in the northern Baltic Sea (**III**). The abundance and range of reed belts have especially increased in the outer areas of the south-western coast of Finland due to the general eutrophication of the Baltic Sea (Roosaluste 2007). During the reproduction period of spring-spawning fish species, the previous year's reeds form the main shallow vegetated littoral habitat available, since the breaking ice removes other perennial littoral vegetation and macroalgae, and the growing

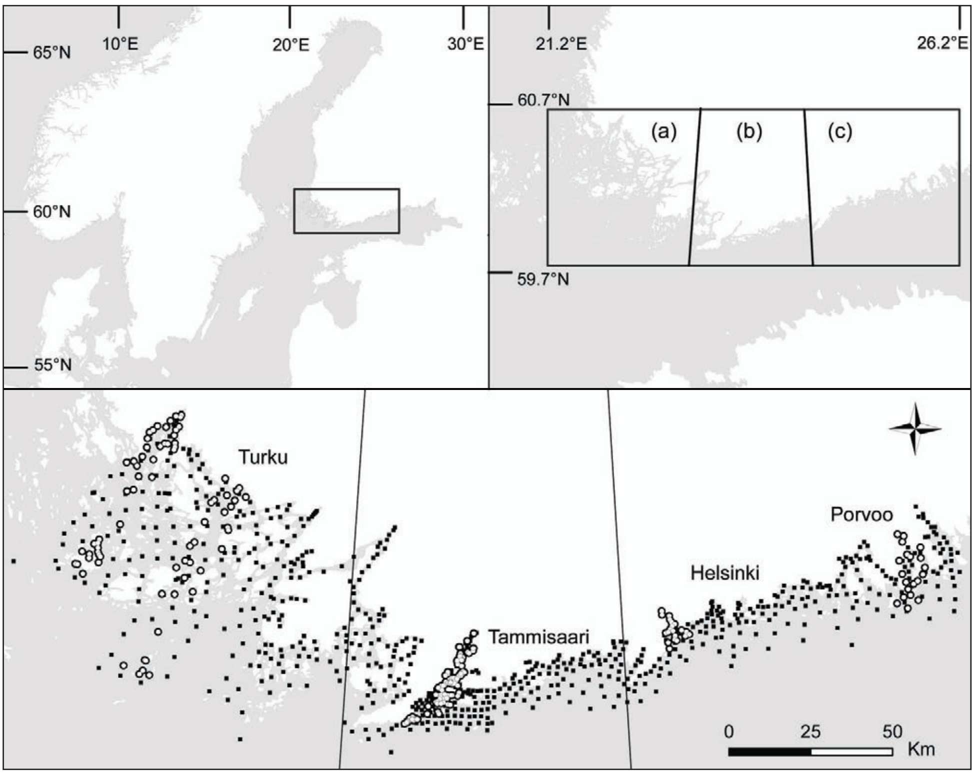

Fig. 1. Location of the study area and the three sub-areas (a = Archipelago Sea, b = Western Gulf of Finland, c = Central Gulf of Finland) in the northern Baltic Sea, and the sampling sites (filled squares = sampling of the abiotic variables salinity and Secchi depth as a basis for subsequent interpolations, white circles = sampling of early life stages of fishes and environmental variables).

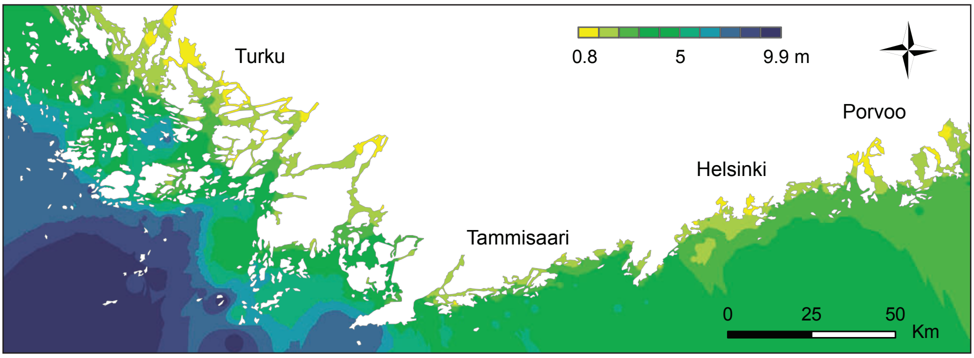

Fig. 2. Interpolated map showing the Secchi depth gradient in the study area during early May.

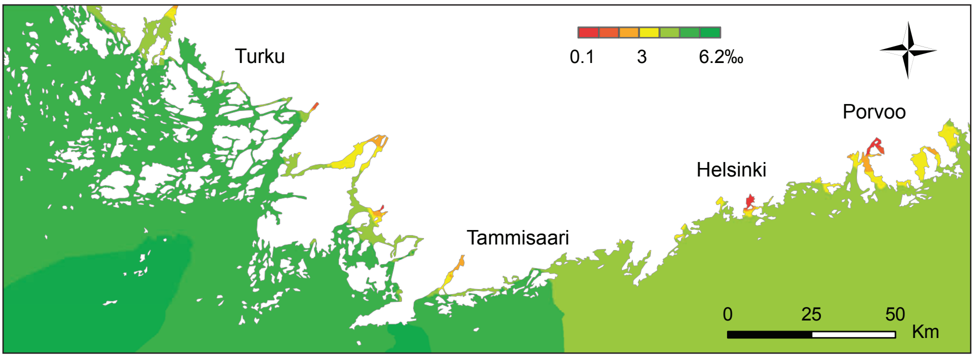

Fig. 3. Interpolated map showing the salinity gradient in the study area during early May.

season of annual plants and algae has not yet begun. The perennial reeds extend from the littoral zone to a depth of usually 1.5 m, and new growth arises annually (Roosaluste 2007).

FIELD SURVEYS ON THE EARLY LIFE STAGES OF FISHES

Early life stages of fishes (eggs, larvae) were surveyed during 2004–2009 at a total of 265 littoral sampling sites, each consisting of a 100-m-long stretch of shoreline (Table 1). The sampling sites were distributed along a series of five transects incorporating exposure, salinity, temperature and turbidity gradients between the innermost bays and outer archipelago areas (Fig. 1). The selection of the sites was conducted by random sampling within the reed-covered shores along the transects so that the full range of the environmental gradients was encompassed. In 2006 and 2008, other habitat types

Table 1. Sampling years and number of field survey sites where the early life stages of fish and environmental variables (ELSF sites) were surveyed and environmental predictor variables forming the basis for subsequent interpolations (env. pred sites) were recorded in the Archipelago Sea, western Gulf of Finland and central Gulf of Finland area.

Area	Year	No. of ELSF sites	No. of env. pred. sites
Archipelago Sea	2006–2007, 2009	94	252
Western Gulf of Finland	2004–2005, 2007–2009	121	306
Central Gulf of Finland	2008–2009	50	230
In total	2004–2009	265	788

(bladder-wrack-shores, non-vegetated shores) were also sampled to improve the predictive power of the habitat models constructed (**II**, **IV**). Sampling of the early life stages of fishes was conducted between early May and early July each year, and 2–5 visits at abouttwo-week intervals were made to each study site.

Early life stages of fish were sampled by wading in shallow water (< 1.2 m) and searching for them in top-layer of water (30–50 cm) using a white plate and a white scoop. The white plate and scoop method has been developed to sample unevenly-distributed small fish larvae in dense vegetation in shallow water areas close to the shoreline (see **I** and **V** for details). It is a rapid, simple and cost-effective method and can be used to determine the presence or absence of the early life stages of fish (eggs, larvae) at the study sites. Furthermore, with a fixed sampling effort and time, it is possible to compare the total number of larvae per species observed at each sampling site per visit. But since these numbers are rough estimates, they should be treated as relative abundances. At each site and visit, 100 m of shoreline was checked during a half an hour sampling period, performed by two persons. The larvae were searched for horizontally along the entire 100 m of the reed belt, starting from the shoreline at one end of the site and proceeding through the cut-down and flattened previous year's reeds in the inner shallow part of the reed belt until 100 m of shoreline had been checked and the other end of the site was reached. The search then continued back again, slowly proceeding through the newly-grown reeds in deeper water, and this deepening zig-zag pattern was continued until the outer edge of the belt at a water depth of approximately 1.2 m was reached. The width of the surveyed area varied approximately between 10 m and 50 m. When eggs or larvae were found, they were counted on the white plate or scoop and the surrounding environmental conditions and vegetation were recorded. A few individuals of each species were also always collected with a scoop in order to verify the species identification later in the laboratory. The fish eggs were incubated in the laboratory and identified to species after hatching. In the predictive spatial distribution modelling, only the presence or absence data on the early life stages of pike and roach was used. In addition to the sampling of the early life stages, sampling of young-of-the-year fish in the Archipelago Sea was conducted at 83 sites in 2006, i.e. the same year when early life stages of fish were sampled in the same area. The sampling design is presented in more detail in paper **IV**.

FIELD MEASUREMENTS OF ENVIRONMENTAL CONDITIONS

At each visit to the fish sampling sites, both the abiotic environmental conditions (temperature, salinity, Secchi depth, turbidity, bottom sediment type) as well as biotic variables (reed belt characteristics, vegetation, availability of prey in some cases, larvae of other species present) were recorded (**I–V**). The availability of zooplankton prey, i.e. density and species composition, were measured at 43 littoral sampling sites in the Archipelago Sea in 2006 (for details see **II**). In addition, water temperature loggers were placed at some of the study sites to monitor the surface water temperature during the sampling periods (**I**). Statistical tests such as ANOVA and correlation analysis (**II**) and principal component analysis (**II**, **V**) were employed to compare the environmental conditions and differences in average values between sites.

MAPS OF ENVIRONMENTAL PREDICTORS

In order to obtain GIS layers of the environmental predictor variables used in the models (**III**, **IV**), a survey aimed at recording the large-scale environmental gradients was conducted in the entire study area in 2007–2009. In addition to the littoral fish and environmental data sampling sites, additional data on salinity, Secchi depth and temperature were collected from 788 sites evenly covering the study area (Fig. 1, Table 1) during the first two weeks in early May each year. These point data on the predictor variables were interpolated to produce continuous map layers using inverse distance weighting (power 2) with a high 25-m spatial resolution in a geographical information system (Figs 2 and 3). The IDW interpolation method was selected based on the assumption that the evenly distributed points were influenced most by the nearby points and less by the more distant points. Validation of the interpolated predictor layers was carried out using calculations of the root mean square error (RMSE) against temperature, salinity and Secchi depth measurements collected simultaneously with the sampling of early life stages of fish from same or previous years (early May) and by visual inspection of plots of field measurements versus interpolated values, and the most representational interpolation maps were selected for spatial predictive modelling. The RMSE gives an overall accuracy measure showing the difference between predicted and observed values, using the same unit as the measurements. The precision estimates (RMSE) between interpolated and observed salinity and Secchi depth for the entire study area were 0.46 ‰ for salinity (N = 276) and 1.08 m (N = 203) for Secchi depth. The inter-annual temperature variation between the sampling of larvae and collection of abiotic variables was too large for successful interpolation and hence excluded from further modelling. In addition to the interpolated predictor layers, already available GIS maps of wave exposure (high 25-m spatial resolution, Isæus 2004), sea surface turbidity (high 75-m spatial resolution, Finnish Environmental Institute) and reed belt locations (high 0.5-m spatial resolution, **III** and moderate 250-m spatial resolution, Pitkänen et al. 2007) were also used.

PREDICTIVE SPATIAL DISTRIBUTION MODELLING OF REPRODUCTION HABITATS OF PIKE AND ROACH

The modelling efforts aimed at producing statistical models that linked the occurrence of early life stages of pike and roach to their surrounding environmental conditions. Two types of logistic modelling approaches, logistic regressions (**I**, **II** and **III**) and generalized additive models (**IV**), were constructed to examine the association between the presence or absence of the early life stages of pike and roach and the environmental predictors, and are presented in more detail in the respective papers. In order to produce probability maps showing the potential reproduction habitats of pike and roach, the final statistical models (logistic regressions, GAM) and the interpolated predictor variables (salinity, Secchi depth, wave exposure) were exported to a geographical information system and used to calculate cell-specific probabilities for the occurrence of early life stages of pike and roach (**III**, **IV**). A description of how the work proceeded can be seen in Figure 4. The extent and the spatial resolution of the outcome predictions were the same as the lowest extent and spatial resolution of the explanatory variable maps. Finally, the model predictions, i.e. probability maps, were constricted to reed-covered shores alone, since this was the only habitat type where the early life stages of pike and roach have been found (**III**, **IV**).

Validation of the spatial distribution models and the outcome probability maps constructed only for a specific study area was conducted during the model building by estimating the accuracy of the model performance in practice using threshold-independent measures (e.g. classificatory power, ROC plots) as described in paper **III**. However, when the distribution maps constructed in a study area were exported to a geographically different area, external validation of the exported probability map based on an independent dataset was conducted as described in paper **IV**.

CONSTRUCTION OF SUMMARY REPRODUCTION HABITAT MAPS

In addition to the predictive spatial distribution modelling presented in papers **I**, **II** and **IV**, summary models were constructed describing the distribution of the reproduction habitats of

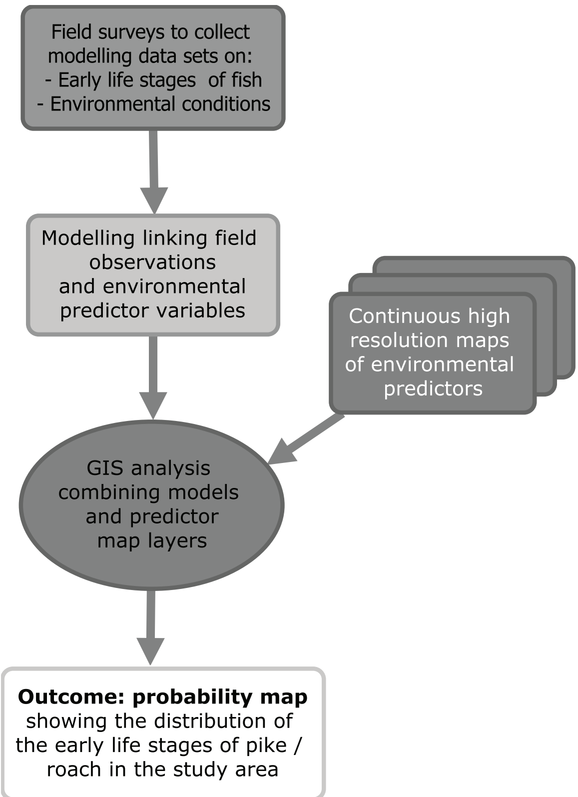

Fig. 4. A scheme showing the steps in the predictive spatial distribution modelling.

roach in the entire study area and of pike in the three sub-areas (a - Archipelago Sea, b - Western Gulf of Finland, c - Central Gulf of Finland, Fig. 1). The whole dataset of several years (2004–2009) and several areas (five transects) was used in these summary models. As a consequence, the summary models gained wider applicability for this specific area because of the wider range of values of the explanatory variables. Moreover, since data from several years and sub-areas were used, the models described more accurately the average extent of the reproduction habitats of pike and roach on the south-western and southern coasts of Finland and not just the situation for one specific year or sub-area. The summary models were constructed as logistic regression models described in paper **III**. Thus, the occurrence (presence/absence) of fish eggs and larvae at the study sites were binary response variables, and the site-specific potential explanatory variables (salinity, temperature, Secchi depth, turbidity, wave exposure) gained from the interpolated predictor variable maps were used as continuous variables. Models with various combinations of explanatory

Table 2. Summary of assessment statistics for summary predictive spatial distribution models of early life stages of roach (entire study area) and pike (sub-areas a-c). The formula of the logistic regression model with one explanatory factor is: $\pi(x) = 1/(1+e^{-(\alpha+\beta x)})$, where, in this case, $\pi(x)$ is the probability of occurrence of early life stages of pike/roach at a certain Secchi depth/salinity (x), and α and β are estimated model parameters. Model performance is given as the area under the curve value of the receiver operating characteristic (ROC) plots. Sensitivity and specificity were calculated after cut-off values maximising the correct classification rate.

	Roach	Pike (a)	Pike (b)	Pike (c)
α	9.805	4.462	2.563	3.550
β	-2.236	-0.714	-1.204	-1.549
N	247	61	64	40
ROC	0.951	0.862	0.781	0.771
Correctly classified	0.879	0.902	0.719	0.750
Sensitivity	0.847	0.959	0.909	0.903
Specificity	0.907	0.667	0.516	0.444

variables and interactions were constructed, but in order to select the model that explained most variation using the smallest number of variables, a backward stepwise procedure was used to select variables for the model among the main effects and the first-order interactions. A significance level of 0.05 was used as a criterion for a variable to remain in the model and the selection was based on the Akaike information criterion (Akaike 1974). The overall goodness-of-fit of the models and prediction accuracy were assessed and validated with regard to the area under the curve value of receiver operating characteristic (ROC) plots (Table 2). ROC values are threshold-independent and range between 0.5 and 1 (Fielding and Bell 1997). Following the classification of Maggini et al. (2006), values below 0.7 were regarded as poor, 0.7–0.9 as reasonable and above 0.9 as very good considering the discriminatory ability. The classification power and uncertainty estimation of the models were evaluated in more detail with classification tables (Boyce et al. 2002) by comparing the observed and predicted responses (occurrence of early life stages of pike/roach) and the sensitivity (proportion of observations correctly predicted as presence) and specificity (proportion of observations correctly predicted as absence) of the models. Here, a jack-knife approach (Efron and Tibshirani 1991) was used to reduce the bias of classifying the same data from which the classification criterion was derived. The final summary models were exported to a geographical information system and used to calculate cell-specific probabilities, the outcomes being summary probability maps with 25-m spatial resolution showing the distribution of the reproduction habitats of pike and roach in reed-covered shores in the entire study area (Figs 5 and 6).

RESULTS AND DISCUSSION

This section of the thesis presents the main study findings (1–6). Each finding is followed by a short discussion reviewing the original results and comparing them with studies conducted elsewhere.

1. The white plate and scoop method with standardized sampling effort and time was demonstrated to be a functional field survey method for detecting the early life stages of fishes in shallow, vegetated littoral shores.

The white plate and scoop method proved to be an easy, simple and cost-effective field survey method that was functional in dense vegetation and shallow water (depth < 1.2 m) close to the shoreline (**I**). It can be used to detect both fish eggs and larvae, i.e. spawning and larval habitats, of several fish species in the shallow littoral shores of the Baltic Sea area (**V**) and has further potential to be used as a littoral survey tool in other shallow, vegetated coastal or estuary areas. Earlier, the white scoop method has been used to observe burbot (*Lota lota*) larvae in an archipelago area in the Gulf of Bothnia, northern Baltic Sea, and in inland waters (Hudd et al. 1983, Urho et al. 1990). The other methods used for sampling the early life stages of fishes are not suitable for sampling in dense vegetation (e.g. beach seining, trawls, see Aneer et al. 1992), cannot be operated in brackish and saline waters (e.g. electro-fishing, see Zalewski and Cowx 1990) or have been developed to sample older life stages, i.e. young-of-the-year juvenile fishes (detonation method, gillnets with small mesh sizes, see Lappalainen and Urho 2006, Snickars et al. 2007), and therefore aim at surveying the nursery areas or habitats for older life stages.

Compared to earlier studies, here a fixed 100-m-long stretch of vegetated shoreline was used as a sampling unit with a fixed sampling effort and duration, and it was therefore possible to compare the total number of larvae per species observed at each sampling site per visit (**I**–**V**). Since the larval abundances are, however, estimates and the white plate method therefore semi-quantitative, we treated the results as relative abundances and only binary presence/absence data were used in the modelling. Predictions based on binary data for species with high detectability, such as pike and roach, have generally been found to perform better and have higher predictive abilities than presence only data (Hirzel et al. 2001, Brotons et al. 2004, MacLeod et al. 2008). Moreover, presence/absence approaches have been found to perform better than abundance models (Francis et al. 2005). However, it is essential that any absence data used for such presence/absence modelling are accurate and contain as few false absences, i.e. locations where a species occurs but for some reason was not detected during data collection, as possible (Hirzel et al. 2002). As shown in paper **V**, the timing for the occurrence of the early life stages varied between fish species, and differences between years may also be substantial. Therefore, each study site was always visited several times (2–5) to minimize the risk of false negative observations.

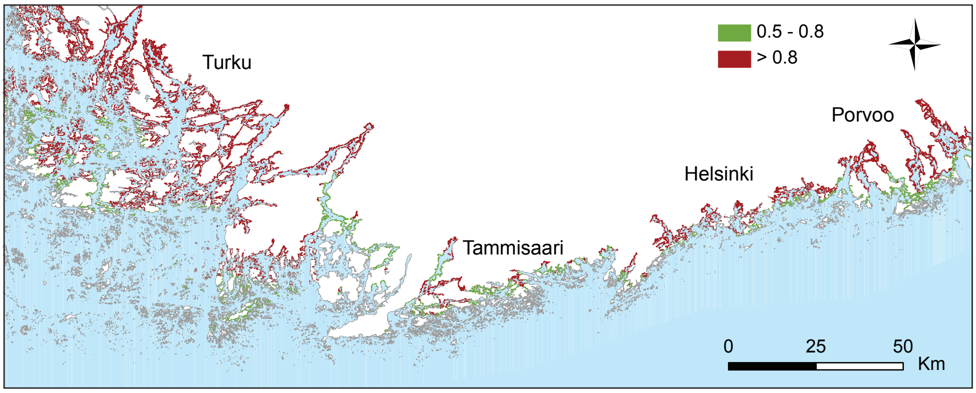

Fig. 5. Modelled spatial prediction of the habitat distribution of the early life stages of pike presented as probabilities of occurrence (0.5-0.8; > 0.8).

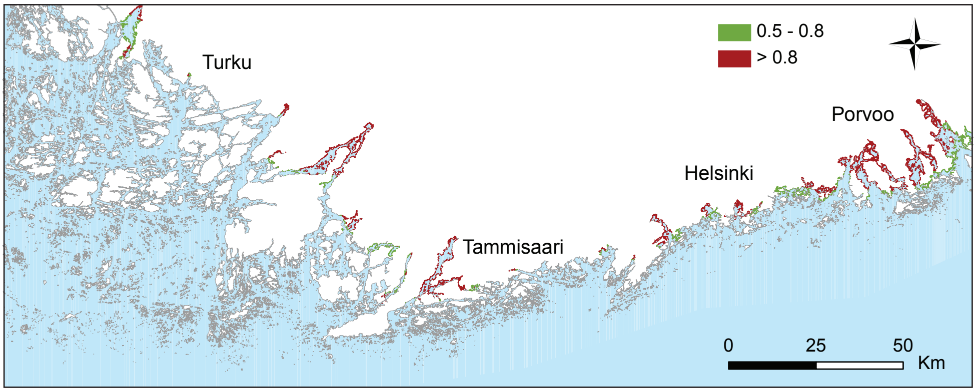

Fig. 6. Modelled spatial prediction of the habitat distribution of the early life stages of roach presented as probabilities of occurrence (0.5-0.8; > 0.8).

2. The reproduction habitats of pike were limited to the sheltered reed- and moss-covered shores of the inner and middle archipelago, where suitable zooplankton prey are available and the influence of the open sea is low.

According to the results, reed-covered shores in the inner and middle archipelago area formed the key reproduction habitats of pike (**I**, **II**, Fig. 5). The early life stages of pike were especially abundant in the inner archipelago and bay areas, in contrast to the outermost archipelago, where they were absent (**II**, **IV**). In the Gulf of Bothnia, north of this study area, the inner archipelago and especially the river mouths and small coastal lakes or ponds connected to the sea have also been reported to be locally important reproduction areas for pike (Urho et al. 1990, Lehtonen and Hudd 1990). Furthermore, in this study, pike were shown to reproduce only on reed belt shores (**I**) and not in the surrounding coastal habitat types that were sampled (**II**, **IV**). In the reed habitats, especially in the inner archipelago, suitable zooplankton prey were more abundant and environmental conditions more favourable, e.g. water temperature was higher compared to other coastal habitat types studied (**II**). Pike eggs and newly-hatched larvae were significantly more abundant within reed belt shores where moss was also found than within reed belts without moss (**V**), and the occurrence of moss therefore indicated an especially competent reed-covered spawning habitat. On the other hand, the empirical results of this thesis disprove the persistent assumption of bladder wrack forming a reproduction habitat for pike in the coastal area of the northern Baltic Sea (**II**), as has earlier also been shown experimentally (Engström-Öst et al. 2007).

The pike is one of the most common predatory fish species in the northern hemisphere (Raat 1988) and it is a target species for the coastal recreational fishery. Lately, however, locally decreasing trends in pike catches and stocks have been reported in several coastal outer archipelago areas in the northern Baltic Sea (Westin and Limburg 2002, Nilsson et al. 2004, Lehtonen et al. 2009), and further studies have revealed a widespread recruitment failure in areas exposed to the open sea on the Swedish side of the northern Baltic Sea (Nilsson et al. 2004). Also in this study, no early life stages of pike were observed in the outer archipelago (**I**, **II**, **IV**, **V**). The poor survival and recruitment of the early life stages of pike in the narrow reed belts were connected to the harsh environmental conditions, as the outer archipelago areas were more vulnerable to the effects of upwelling and currents from the open sea and less vulnerable to the turbid runoff waters from land compared to the sheltered inner bays (**II**). Salonen et al. (2009) have also reported similar results. The influence of the open sea on the outer reed belts can be seen in sub-optimal feeding conditions, i.e. lower prey availability (**II**), and in more pronounced water-level fluctuations, which cause temporary drying of the narrow spawning sites (**I**), as also has been reported in earlier studies (Johnson 1957, Inskip 1982). Another possible factor contributing to the decline of pike in the outer archipelago could be predation on older pike larvae and juveniles that migrate offshore from the main reproduction habitats by other fish species (Lehtonen et al. 2009). Therefore, it seems that pike cannot benefit from the recent increase in the extent of the reed-covered habitats (**I**) that has taken place in the outer archipelago (Roosaluste 2007). However, it remains unclear whether the situation has changed during recent decades, i.e. whether pike reproduction in the outer archipelago has lately become unsuccessful, or whether the outer archipelago pike have always immigrated from the inner archipelago, where pike production may have been stronger also in the past (Lehtonen et al. 2009).

Modelling the reproduction habitats of pike turned out to be challenging. There were two main reasons for this: (1) the best performing predictor variables, Secchi depth and salinity, had only an indirect influence on the occurrence of early life stages of pike (**I**, **IV**), and in addition, (2) the range of the environmental conditions significant for pike varied between different parts of the coastal study area (Figs 2 and 3). Consequently, the range of environmental conditions at locations where pike were present also varied in different parts of the coastal study area (**IV**). Thus, the summary map showing the predicted reproduction habitats of pike (Fig. 5) consisted of three parallel models altogether: one for the Archipelago Sea area (a), one for the western Gulf of Finland area (b) and one for the central Gulf of Finland area (c). In these summary logistic regression models, the only site-specific variable significantly ($p < 0.001$) explaining the occurrence of early life stages of pike was Secchi depth, which was measured at the beginning of May. In the GAM model, salinity was also used as a predictor variable (**IV**), but since the salinity gradient correlated with the Secchi gradient in the study area, both variables could not be used as predictors in the logistic regression models. However, all the pike models constructed provided a good fit with a reasonable to good discriminatory ability (Table 2; **IV**), and a lower Secchi depth indicated a higher probability for the occurrence of early life stages of pike. Secchi depth, despite its indirect predictive nature, was shown be a useful abiotic predictor in this type of modelling as it (1) correlated with prey density in reed belts (**II**) and (2) indicated the influence of the open sea and, furthermore, was rather easy and cost-effective to determine by remote sensing methods.

3. The reproduction habitats of roach were limited to the very sheltered reed-covered shores of the innermost bay areas, where salinity remained low during the spawning season due to freshwater inflow.

According to the results, in the south-western and southern coastal areas of Finland, in the Northern Baltic Sea, roach only successfully reproduced in the innermost bays and archipelago areas (Fig. 6), where freshwater runoff has a strong influence on salinity in the spring. In the inner archipelago, roach reproduced on almost all vegetated shallow shores where reed belts were present and salinity remained below 4.0‰ in early May (**III**, **V**). Our results support earlier laboratory studies, which have indicated that Baltic roach reproduction is unsuccessful in salinities exceeding 3.5‰ (Jäger et al. 1981, Klinkhardt and Winkler 1989). In the Quark area of the northern Baltic Sea, roach have also been reported to only reproduce in those coastal areas receiving substantial inputs of freshwater (Urho et al. 1990, Karås and Hudd 1993). In this area, however, salinity stays below 4.0‰ through the entire archipelago zone. Therefore, other limiting factors such as harsh temperature conditions (short growth season) and possibly also food limitations, may limit roach reproduction in the outer archipelago. According to our results, roach can occasionally also reproduce in the intermediate archipelago zone in the north-western Gulf of Finland, but probably only in sheltered reed-covered inlets where local freshwater sources, such as small ditches, reduce the salinity and water exchange is low (**III**). Sensitivity to salinity makes roach reproduction more confined to the inner bay areas than many other freshwater fish, although the results of this study indicate that some other cyprinids, such as bream and white-bream, could also be as limited by salinity as roach during reproduction (**V**). Nevertheless, the considerably limited reproduction areas of roach produce very abundant coastal populations of adult roach (Lappalainen et al. 2000, Ådjers et al. 2006) and it seems that roach juveniles begin to disperse outside the inner reproduction areas already during the first summer.

In the future, climate change is predicted to increase rainfall in the northern Baltic Sea region (Winsor et al. 2001), change the spring freshwater runoff pattern and reduce the salinity of the Baltic Sea (Meier 2006, Meier et al. 2006). According to our results, the most likely outcome is a spatial increase in the extent of roach reproduction habitats to reed belt shores in areas where salinity is currently too high (> 4‰) for reproduction, and thus a further increase in roach population (**III**). For instance in the Tammisaari archipelago, in the western Gulf of Finland, the coastal shoreline suitable for roach reproduction could increase at least threefold, since only 32% of the reed-covered shores are currently available for roach reproduction (**III**). However, since the exposure differences will remain, it may be that roach will not be able to reproduce in the outermost archipelago zone. MacKenzie et al. (2007) have also suggested that climate change could alter the distribution of freshwater fish species in the Baltic Sea due to changes in the extent of the reproduction habitats. Moreover, climate change is expected to cause wider distribution shifts in marine fish species, but mainly due to changes in water temperatures, both in the Baltic Sea (Lehtonen 1996, MacKenzie et al. 2007) and in other estuarine and marine areas (Kennedy 1990, Perry et al. 2005, Rijnsdorp et al. 2009). In addition to the climate change effects, the northern Baltic Sea has become highly eutrophicated (Cederwall and Elmgren 1990, Bonsdorff et al. 1997, Lundberg et al. 2009), which has been suggested to be beneficial to roach and other cyprinid species (Lappalainen et al. 2001) already during the first summer (Sandström and Karås 2001). Eutrophication has affected the bottom quality, water turbidity and algal growth, while reed belts have become more common and increased in size in many coastal areas (Roosaluste 2007). The combined effects of these environmental changes will, therefore, most likely benefit roach, whose increasing abundance is expected to have widespread ecosystem effects. Along the northern Baltic Sea coasts, the feeding areas of adult roach extend nowadays also to the outer archipelago, and an increased abundance of roach with their high predation pressure will negatively affect, for instance, the populations of blue mussel (*Mytilus edulis*) (Lappalainen et al. 2005, Westerbom et al. 2007). An increasing abundance of roach and other cyprinids has also been regarded as harmful to fisheries, since roach are less valued and have only minor importance for the recreational fishery.

Since salinity has such a direct physiological influence on the reproductive success of roach (Jäger et al. 1981, Klinkhardt and Winkler 1989), the distribution of the early life stages of roach was straightforward to model and thus well described in the entire study area (Fig. 6) with one logistic regression model (**III**). In this model, the only site-specific variable significantly ($p < 0.001$) explaining the occurrence of early life stages of roach was the spring surface water salinity, which was measured at the beginning of May. The model provided a good fit of the data and had very high discriminatory ability and stability (Table 2, **III**). In the more complex GAM model that was constructed, Secchi depth and wave exposure were also used in addition to salinity to predict the distribution of roach larval habitats. This model also had very good transferability due to the direct effect of salinity and, thus, the small window of presence of early life stages of roach along the environmental gradients (**IV**).

4. Reed belts form especially important reproduction habitats also for several other freshwater fish species in the northern Baltic Sea.

The early life stages of ten fish species were recorded from littoral reed-covered habitats (**V**), and they comprised more than 30% of the fish species with spring or summer larval stages occurring in the studied coastal areas. In particular, freshwater fish species such as pike, burbot, roach and other cyprinids, which have a known preference for vegetated littoral areas during their early life stages (Mann 1996, Weaver et al. 1997), were shown to extensively exploit the reed habitats as spawning or larval areas (**V**). Reed-covered shores form the prevailing vegetated habitat type in the coastal northern Baltic Sea during early spring, although some other plants, such as *Myriophyllum*, *Schoenoplectus* and *Potamogeton* species, may grow within reed belts as sparse patches. For instance, in the Tammisaari archipelago, reed belts cover 58% of the shoreline in the inner bay area, 32% in the intermediate archipelago and 9% in the outer archipelago (**III**). Reed belts were also shown to maintain almost 3 °C higher temperatures (**II**), almost 10-times higher prey densities than other surrounding littoral habitats (**II**) and 20–280 times higher prey densities than have been reported from the pelagic waters of the northern Baltic Sea (Viitasalo 1992). Earlier field observations (Jeppesen et al. 1994) and experimental studies (Schriver et al. 1995) have also demonstrated that submerged macrophytes enhance zooplankton density, and the preferred prey species, cladocerans and copepods, have particularly been shown to be more abundant in the vegetated littoral zone than in the open sea (Jeppesen et al. 1998, Geraldes and Boavida 2004., Telesh 2004). Reed belts have also been shown to have high importance as nursery habitats for juvenile fish (Snickars 2008).

However, strong spatial differences in environmental conditions and vegetation cover were detected between the inner and outer reed belt shores due to exposure gradient (**II**, **V**). This influenced the occurrence of fish larvae, since some species had more limited environmental requirements than others. Thus, the reed belt shores in the inner bay areas with a low salinity, high water temperature and dense vegetation were emphasized as especially productive fish reproduction areas in this study (**V**). Previous investigations conducted in the northern Baltic Sea (Urho et al. 1990, Lehtonen and Hudd 1990, Karås and Hudd 1993, Snickars 2008) and globally in other estuarine and coastal marine systems (Beck et al. 2001) also support this finding by emphasizing the importance of coastal bays, lagoons and shallow water areas as productive areas. The regional importance of the reed belt shores in the northern Baltic Sea arises from the scarcity of other suitable vegetated habitats, especially in the early spring. Therefore, temperate reed habitats, especially in inner bay areas, can be considered as regionally significant productive systems. They may be comparable even to marshlands or mangrove swamps, which have been recognized as key fish reproduction habitats in subtropical and tropical latitudes (Weinstein 1979, Boesch and Turner 1984, Manson et al. 2005).

5. Large-scale predictive spatial distribution maps of the reproduction habitats of pike and roach were successfully constructed by combining statistical models linking the occurrence of early life stages to environmental conditions and a few and easily-measured spatial predictor variables in a geographical information system.

Predictive spatial species-habitat distribution modelling was successfully used here to extrapolate field survey information to continuous maps identifying the areas of particular importance as reproduction habitats for pike and roach (**III**, **IV**). Due to practical and financial constraints, it is impossible to investigate all potentially suitable coastal areas for a species of interest solely with field surveys. Therefore, predictive spatial distribution modelling was needed and the work proceeded in four steps (Fig. 4).

The first step when mapping fish reproduction habitats was to select the sampling design and conduct the field surveys to collect the modelling data sets. Here, we obtained as representative a data set as possible by using environmental information to stratify sampling, as suggested by Hirzel and Guisan (2002). Based on the exposure characteristics of the study area, a series of five gradsect transects (Austin and Heyligers 1989) incorporating significant environmental gradients were selected to represent the spatial environmental variability present in the study area. This was carried out to ensure that the widest possible range of environments were sampled as evenly as possible with reasonable constraints on travelling time and costs and to cover also areas outside the presence range of the species (**IV**). A well-planned sampling strategy in field surveys ensures that all potentially useful explanatory variables are sampled, can considerably improve model results and reduce the risk of inaccurate, biased or imprecise predictions (Guisan and Zimmermann 2000). Sampling should preferably also cover several years to catch the annual variation in the distribution and extent of the reproduction habitats, as was also conducted here (**III**, **IV**).

In the next step, modelling was used to link the field observations of early life stages of pike and roach to their environment. Species-specific statistical models were successfully developed using two alternative logistic approaches and a few spatially available abiotic predictor variables (**III**, **IV**). The first approach, logistic regression modelling, has been widely used in modelling habitat suitability and species distributions (Guisan and Zimmermann 2000, Stoner et al. 2001). The second approach, GAM modelling (Hastie and Tibshirani 1990), is more complex but has the advantage of better handling of highly non-linear relationships that are common in nature, and is consequently nowadays the most common and well-developed method for modelling fish habitats (Valavanis et al. 2008). However, due to the high smoothing capability, overfitting can be a problem with GAM models. The final selection of explanatory variables (salinity, Secchi depth, wave exposure) was based on statistical consideration and knowledge of the biology and ecology of the species, and both direct and indirect predictor variables were used in the models (**III**, **IV**). The poor availability of spatial predictors was a limiting factor in the modelling and, therefore, many biotic predictors regarding the basic biological and ecological requirements of the larvae had to be excluded from the analyses. The use of direct predictors ensures that a model is more general and applicable to large areas (Guisan and Zimmermann 2000), as was shown to be the case with salinity, which has a direct physiological effect on the distribution of early life stages of roach (**IV**). However, the availability of high-resolution spatial predictor variables is often limited and the use of indirect predictors is therefore often necessary. The number of the predictor variables selected should, however, be kept within reasonable limits, as was done here, since the inclusion of a large number of explanatory variables in a model may lead to overfitting, reducing the predictive capacity and generality (Clark 2005).

In the third step, continuous high-resolution maps describing the environmental predictors in the study area were constructed by interpolating field observations or by utilizing remote sensing. Finally, in the fourth step, the large-scale distribution of the reproduction habitats of pike and roach were successfully visualised on a map by importing the constructed models into a geographical information system and combining them with spatial environmental predictor variable layers, such as salinity, turbidity, wave exposure and vegetation (**III**, **IV**). The constructed models were based on large empirical field data sets and therefore predicted the realized ecological niche of the studied species. This may, however, seriously limit the transferability and application of the models in changing environmental situations, as was shown in paper **IV**. Thus, to estimate how accurately the models performed in practice, two types of validation approaches were used: (1) In the first approach, models constructed to describe the distribution of the reproduction habitats of pike and roach in only a specific study area were validated by threshold-independent measures (e.g. ROC plots) during model building (**III**, summary models). This type of validation approach, in addition to the cross-validation, can sometimes be more practical because it allows the use of all available data in the modelling process, i.e. it covers the entire environmental variability present in the study area and also in areas outside the presence range of the study species, as Lehmann et al. (2002) have indicated. However, without external assessment (Elith et al. 2006) of the generality of the modelled reproduction habitat preferences, the distribution models cannot be transferred to new areas. Therefore, (2) in the second approach used in paper **IV,** the maps of the potential distributions constructed in the training area were exported to an external testing area and the validation of the exported maps was based on independent, well-structured presence/absence data sets, as Elith et al. (2006) have suggested. This type of external validation enables the transfer of the models to new areas, and it is especially needed when dealing with indirect predictor variables in a predictive context, since the relationship between the indirect and the underlying direct variables may change with region or time (**IV**).

The marine environments are complex, heterogeneous and dynamic; over a fixed background of bathymetry and seabed substrate, environmental conditions and prey availability vary in time (diurnally, seasonally, interannually) and space (vertically, horizontally) at various scales (Valavanis et al. 2008). Therefore, many marine fish species, in particular, have wide distribution ranges and respond to environmental variation by changing their distribution patterns and habitat use (Perry et al. 2005, Laurel et al. 2007, Morrell and James 2008) and by altering their reproductive input (Billard 1981, Craig and Kipling 1983, Pecquerie et al. 2009). Consequently, this makes it more challenging to predict the distribution of fish species and their habitats in every combination of time and space using a single model. The reproduction habitat maps constructed here (Figs 5 and 6, **III**, **IV**) describe the distribution of the potential reproduction habitats of pike and roach in the coastal study area based on the occurrence of early life stages and environmental conditions of the specific study years. Thus, the largest uncertainty in these probability maps results from the limited time frame of the field surveys; both the statistical models and especially the interpolated predictor maps were in some sub-areas based on field data sampled during only one year. However, the environmental conditions, such as the salinity gradient or water level, may vary between years and thus influence the extent and quality of the reproduction habitats of roach and pike, respectively. Therefore, the static nature, predictive capability, spatial resolution and accuracy of the predictive spatial distribution models developed should always be carefully interpreted for end-users, since decisions based on these maps may have long-term consequences.

6. The lack of high-resolution spatial predictors limits coastal fish reproduction habitat mapping and distribution modelling.

The current lack of accurate large-scale, high-resolution spatial data on the predictor variables, such as submerged vegetation, salinity, surface temperature and bottom sediments, is a considerable limitation for predictive spatial distribution modelling of shallow coastal waters. In this study, most of the GIS layers of the predictor variables used (salinity, Secchi depth) were constructed by interpolating field observations that were gathered at exactly the right time, i.e. within 1–2 weeks, since environmental conditions may vary considerably between seasons, and with a considerable sampling effort on an area per year basis (**III**, **IV**). However, the abiotic data would at best consist of average values gained from several years to catch the interannual variations in the environmental conditions. Unfortunately, no continuous maps for parameters such as salinity determined by remote sensing methods are currently available, and field sampling must still be carried out as basis for subsequent interpolations. Some variables, e.g. Secchi depth, could also be mapped by GIS modelling techniques, i.e. by developing suitable proxy variables from already existing spatial data sets (Snickars et al. 2010), such as wave exposure (Isæus 2004) and water distance from the baseline. However, such proxy variables will only reflect the quality, spatial resolution and extent of the input data.

Remote sensing was used in this study to map the reed belt locations along the shoreline (**III**). Aerial photographs were initially used and proved to be accurate, with a high spatial resolution (0.5 m), but the visual interpretation was quite laborious and therefore expensive as a large-scale mapping method (**I**, **III**). It can also be challenging to find up-to-date aerial photographs. Therefore, an alternative and more efficient approach to attain large-scale maps of reed belt locations was sought and satellite imagery, such as Landsat TM/ETM+ frames with 250-m spatial resolution and supervised computer-based interpretation provided by Turku University (Pitkänen et al. 2007) was used (**II**, **IV**, **V**). However, the moderate 250-m spatial resolution of these satellite images was relatively coarse when modelling the distribution of fish reproduction habitats in the heterogenous coastal environment. Thus, the remote sensed vegetation data was only used to restrict the model predictions, i.e. probability maps, to reed-covered shores.

Satellite imagery provides an extensive knowledge base of sea-surface conditions, allowing the mapping of important ocean processes that influence species distribution (Valavanis et al. 2008). However, the moderate to low spatial resolution (> 200 m) is a disadvantage of most satellite images, and with images of high resolution (0.5–35 m) costs will again increase, since the number of images needed to classify the coastal area increases (Pitkänen et al. 2007). The effect of spatial resolution on the precision of the results, as well as the implementation of datasets with moderate to low spatial resolution to local studies, especially to heterogeneous environments, should however be considered carefully and site specific (Gertner et al. 2002, Sprintsin et al. 2007). Low spatial resolution data may be valid in studies conducted in oceans, but the large environmental gradients and the extensiveness of the archipelago zone in the northern Baltic Sea demand an especially high spatial resolution for the coastal predictor variables. Therefore, efforts to enhance the interpretation of satellite images are warranted and the development of remote sensing techniques in general is of fundamental importance, since water temperature maps could, for instance, also be generated by satellite image interpretation. The sea surface temperature could be a useful predictor variable when mapping and modelling the reproduction habitats of species such as pikeperch (*Stizostedion lucioperca*) or perch (*Perca fluviatilis*), which are known to display large variations in year-class strength due to temperature (e.g. Lehtonen and Lappalainen 1995), or some other coastal species, such as pike or cyprinids studied here.

Due to the large spatial coverage of satellite data, it is easy to extract reproduction habitat maps that expand the sampling area. However, the outcome can sometimes be underestimated or result in biased predictions for areas outside the actual sampling area (Valavanis et al. 2008). Since a model is always based on environmental variables within specific ranges in the sampling area, predictions outside of these ranges might be unrealistic. However, as long as a prediction is made within the known limitations of the study, there are many advantages in using satellite datasets in predictive spatial distribution models.

CONCLUSIONS AND IMPLICATIONS FOR MANAGEMENT

In the research presented in this thesis, the distribution of the reproduction habitats of two freshwater fish species, pike and roach, were surveyed, mapped and modelled along environmental gradients. Rather similar mapping and modelling approaches have generally also been used to describe the distribution of essential fish habitats in other sea areas (Valavanis et al. 2008 and references therein) for both pelagic (e.g. Bellido et al. 2008, Schismenou et al. 2008, Druon 2010) and demersal fish species (e.g. Moore et al. 2009). However, at least three factors characterize the studies described in this thesis and distinguish them from previous studies in other sea areas: (1) the fish reproduction habitats here were limited to very shallow littoral vegetated shores, (2) very strong and large environmental gradients were present in small geographical areas and (3) an extensive and complex archipelago zone defined the coastal study area in the northern Baltic Sea. Two consequences resulted from these factors: firstly, the coastal field surveys had to be detailed and required specific field survey methods that allowed sampling in shallow littoral shores within dense vegetation; and secondly, coastal predictor variables had to be recorded at an especially high spatial resolution and at exactly the right time, and a better availability of high-resolution predictor maps was thus needed.

Continuous fish reproduction habitat maps were, however, successfully constructed for two coastal species, pike and roach. This type of illustrative spatial information offers a practical and valuable tool for efficient management of the heavily exploited coastal zone by promoting the sustainable use and management of the coastal areas (ICES 2004, ICES 2007), aquatic species conservation and habitat protection (Halpern et al. 2005, Sale et al. 2005) and can further be used to maintain the sustainability of fish populations and conserve their associated fisheries by limiting anthropogenic stressors in such habitats, for instance by identifying optimal locations for Marine Protected Areas (Walters 2000) or for disturbed habitat restoration efforts (Fago 1977, Morrow et al. 1997). The reproduction habitat maps constructed here have already been utilized by local fisheries managers when setting local fishing restrictions in the studied coastal area. Furthermore, the results of this study could be used to develop new approaches and tools to assess the effects of both local (e.g. dredging, dumping of dredging masses, coastal construction) and wide-scale (e.g. coastal eutrophication, climate change) environmental change on fish reproduction in the coastal environment. Last but not least, the results of this thesis highlight the importance of coastal reed belts as habitats for early life stages of fish.

Future studies could focus on at least six areas: (1) clarifying the effects of annual variations in environmental conditions and further on the accuracy of the fish reproduction habitat maps; (2) applying the survey, mapping and modelling methods developed in this study to other coastal fish species, including species with pelagic early life stages; (3) studying human-induced threats and their effects on the key reproduction habitats; (4) assessing the effect of grazing cattle on the reed habitats; (5) developing new approaches to plan coastal management actions based on spatial reproduction habitat information to support the sustainable reproduction of species such as the pike, and thus fisheries based on these species; and finally, (6) providing further clarification before linking the spatial reproduction habitat information to stock sizes.

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